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The New Zealand storm-petrel (*Pealeornis maoriana* Mathews, 1932): first live capture and species assessment of an enigmatic seabird

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Abstract The New Zealand storm-petrel *Pealeornis maoriana* Mathews, 1932 was described from 3 specimens collected in the 19th century. Since 1952 it has most commonly been considered a subspecies of Wilson's storm-petrel *Oceanites oceanicus* exhibiting the ventrally streaked "*Pealea*" phenomenon. There had been no recorded sightings of the New Zealand storm-petrel in over 170 years before Jan 2003. Since then, observations off northern New Zealand of storm petrels believed to be this taxon have been made regularly during the austral summer. From observations and photographs, these birds appeared more similar to the New Zealand storm-petrel than to other storm petrel species occurring in the region. However, confirmation of their identity was not possible without capture. In Nov 2005 one was captured off Little Barrier Is, and 3 more were caught elsewhere in the Hauraki Gulf in Jan 2006. Analyses of detailed descriptions, photographs, and morphometric data of these birds provide conclusive evidence that they represent an extant population of the New Zealand storm-petrel. Our analyses of these data and comparison with the New Zealand storm-petrel museum specimens and 17 other Southern Hemisphere storm petrel taxa (subfamily Oceanitinae), lead us to conclude that this species is distinct.

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INTRODUCTION

In Jan 2003 a small black-and-white storm petrel was photographed off Whitianga, Coromandel Peninsula, New Zealand (36° 43′ 45″ S; 176° 01′ 58″ E) (Saville *et al*. 2003; Stephenson *et al*. 2008). In Nov 2003 at least 10 similarly-plumaged storm petrels were seen 2 nm north of Little Barrier Is, Hauraki Gulf, New Zealand (Flood 2003; Stephenson *et al*. 2008). Subsequently there have been 100s of sightings of these storm petrels in the Hauraki Gulf (Gaskin & Baird 2005; *authors unpubl*.). It has been widely considered that these birds indicated the continued existence of the New Zealand storm-petrel *Pealeornis maoriana* (Saville *et al*. 2003; Flood 2003; Brooke 2004; Birdlife International 2006), an enigmatic taxon not accepted by reviews of the order Procellariiformes

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in the late 20th Century (Ornithological Society of New Zealand 1990; Warham 1990; but see Brooke 2004; Onley & Scofield 2007).

Both the Jan and Nov 2003 sightings were initially identified at sea as black-bellied storm-petrels *Fregetta tropica*, and it was only examination of photographs that led to this identification being questioned (Saville *et al*. 2003; Flood 2003). The possibility of the birds being New Zealand storm-petrels (NZSP), the name first proposed by Oliver (1955), was put forward by A.J.D. Tennyson (Museum of New Zealand Te Papa Tongarewa). Following the 1st sighting, white-vented *Oceanites gracilis* and white-throated storm-petrels *Nesofregetta fuliginosa* were discounted due to size and plumage differences (Saville *et al*. 2003). The possibility that the Jan 2003 bird was an aberrantly-plumaged white-bellied *Fregetta grallaria*, black-bellied or Wilson's storm-petrel, *O. oceanicus*, was considered (Saville *et al*. 2003) because *Garrodia*, *Pelagodroma*, *Fregetta*, *Nesofregetta* and *Oceanites* very occasionally exhibit ventral spotting or streaking as variations from the normal plumage (Murphy & Snyder 1952; Oliver 1955; Trimble 1968; Reed 1979; Bourne 1987; Curtis 1988). However, multiple sightings of similarly-plumaged storm-petrels discounted this possibility.

Taxonomic confusion has plagued the NZSP, largely due to the existence of only 3 specimens and the presence of several other storm petrel specimens exhibiting streaked plumage. The collection of the 2 French NZSP specimens in 1827 (kept at the Museum National d'Histoire Naturelle, Paris, France; Nos. 17 (14393) and 18 (14372)) and the British NZSP specimen presented in 1895 (kept at the Natural History Museum, Tring, UK; No. 1895.2.1.11) has been documented by other authors (Bourne & Jouanin 2004; Medway 2004; Bourne *et al*. 2004).

However, during the US Exploring Expedition 1838-1842 visit to Upolu, Samoa (probably during Oct-Nov 1839 (Wilkes 1845)), a ventrally-streaked storm petrel was obtained and named *Thalassidroma lineata* Peale, 1848, the name being subsequently used by Cassin (1858). This Upolu specimen is now kept at the Smithsonian National Museum of Natural History, Washington DC (USNM-A15713). The Peale specimen and one of the Paris specimens (the other seems to have been lost for a time: see Cassin 1858; Godman 1907; Oliver 1930) showed plumage similarities, so Bonaparte (1857) assigned both to *Oceanites lineata* due to similarities he felt they shared with *Oceanites*. Re-examination of the Peale type by Ridgway (1886) led to further revision based on several differences to Wilson's storm-petrel, and he proposed the new genus *Pealea* (hence *P. lineata*).

Godman (1907) was the 1st to publish a plate with a colour illustration of 1 of the Paris specimens by J.G. Keulemans, making mention that both the Paris and London specimens had come from New Zealand waters (he also seemed to know of only 1 Paris specimen). Godman retained *Pealea lineata* and named it Peale's storm-petrel.

A 5th similar storm petrel was collected by R.H. Beck off Huapu Is, Marquesas Is in 1922 (Murphy 1924). Collected whilst feeding in the company of large numbers of *F. grallaria*, this specimen is now held at American Museum of Natural History, New York (AMNH 194110). Upon examination it was concluded to show features intermediate between *F. grallaria* and *F. tropica.* Due to its streaked plumage, it was also included with the other 4 streaked specimens, but this time they were named *Fregetta lineata* (Murphy 1924).

Oliver (1930) concluded that these 4 specimens (he also knew of only 1 Paris specimen) were distinct, referring to them as Peale's storm-petrel *F. lineata* after Murphy (1924). Oliver correctly recognised the Paris specimen's provenance as East Cape.

Mathews (1932) examined 3 specimens (apparently the 2 specimens held in Paris and the 1 now at Tring). Based on similarities among these, and differences from the Marquesan and Samoan specimens, he described the 3 as the new genus and species *Pealeornis maoriana*, with the Tring specimen designated as the holotype. Mathews (1933) provided further description of the specimens, including drawings of a feather, 2 legs, and a plate showing a ventral view of the entire type, and making it clear that the other specimens in the original description were the 2 in Paris. After further examination, Mathews (1936) provided an even more complete description, including several new comments, and photographs showing a leg and dorsal and ventral views of 1 specimen.

The situation seemed resolved, with 3 near identical specimens all originating from New Zealand, and described as taxonomically distinct, until Murphy & Snyder (1952) re-examined the 5 streaked specimens. Based on morphometrics and details of the foot shape, they concluded that the 3 New Zealand birds were a genetically-based pale phase of *O. oceanicus*; that the Samoan specimen was *F. tropica*; and the Marquesan specimen was *F. grallaria*. They linked the streaked plumage of these birds to that of other storm petrels, particularly *F. grallaria*, *N. fuliginosa*, grey-backed storm-petrel *Garrodia nereis*, and white-faced storm-petrel *Pelagodroma marina*: the "*Pealea*" phenomenon (Murphy & Snyder 1952).

However, Oliver (1955) treated all 3 New Zealand specimens as a separate species, New Zealand storm-petrel *Oceanites maorianus*, because, at the time, *O. oceanicus* was thought only to straggle to New Zealand waters (but see Horning 1976; Marchant & Higgins 1990; Petyt 2001; Stephenson

et al. 2008, who provide information on records of *O. oceanicus* in New Zealand waters), and, where abundant, is not known to produce colour varieties. However, the Ornithological Society of New Zealand's Checklist Committee (Ornithological Society of New Zealand 1990) followed Murphy & Snyder (1952), as have most texts since then (e.g. Marchant & Higgins 1990 (although they also suggested the 3 specimens were a form of *F. tropica*) and Shirihai 2002). More recently Holdaway *et al*. (2001) and Brooke (2004) use *O. maorianus*, but Onley & Scofield (2007) and Shirihai (2007) chose to revert to *Pealeornis maoriana*.

In an attempt to determine the identity of the black-and-white storm petrels seen off northern New Zealand since 2003, we set out to capture birds in the Hauraki Gulf. We present information from the first 4 of these birds captured during the austral summer of 2005-06, and provide detailed comparisons with the NZSP museum specimens and other extant Southern Hemisphere storm petrels (subfamily Oceanitinae).

METHODS

The 1st bird was captured serendipitously on 4 Nov 2005 at approximately 2045 h (NZST), when it flew into the lit cabin of former wildlife officer G. Murman's fishing boat anchored in Waimaomao Bay, Little Barrier Is (36° 10′ 10″ S; 175° 05′ 46″ E). It was held overnight, and examined, measured, photographed, banded and released next day. It was checked for ectoparasites and 5 feathers were taken from the breast for molecular analysis.

Two catching trips on 5-6 and 8-10 Jan 2006 were conducted in the Hauraki Gulf at places where, based on previous experience, storm petrels were likely to be found in the prevailing weather conditions (Gaskin & Baird 2005). Storm petrels, as with other species of Procellariiformes, are known to have a well developed olfactory sense (Verheyden & Jouventin 1994), so we used fish oil and fish scraps to attract birds. Thirteen hours were spent attempting to capture birds near 35° 57′ 53″ S; 175° 58′ 53″ E, an area approximately 6.2 nm south-west of the Mokohinau Is, Hauraki Gulf (35° 54′ 21″ S; 175° 06′ 47″ E) during 2 trips consisting of 5 days in total. Weather was similar during the 2 trips, with moderate to rough seas (1-3 m swell), and 10-25 knot SW and SE winds, generally increasing throughout each day.

Several capture techniques were assessed during the 2 trips, with all 3 birds being captured using a net-gun. All birds were banded, weighed (using a 100 g Pesola) and measured using standard techniques (tail length, bill length, tarsus length, mid-toe and claw length) with Vernier callipers to 0.1 mm, except flattened wing chord which was measured using a stop rule to the nearest 1 mm. The brood patch of each bird was also examined. As all birds were banded upon capture, we refer to each by its band number (4 Nov 2005, B-97715; 5 Jan 2006, B-94503; 6 Jan 2006, B-94504; and 9 Jan 2006, B-94505).

All 4 birds were photographed and each was examined for ectoparasites, which were placed into 70% ethanol, and later curated and identified. Morphometric data collected from the captured birds were compared with measurements from the NZSP museum specimens and data from 17 Southern Hemisphere storm petrel taxa (subfamily Oceanitinae) (Table 1). Complete morphological data were not available, so we conducted a multivariate analysis using wing length, bill length, and tarsus length. We standardised all values so that the sum of the values was 0 and standard deviation (SD) 1. Analysis was then conducted using these standardised values. Further, we assessed the amount of variation between morphometric values with each species of storm petrel, combining values for the captured birds and the NZSP museum specimens, and analysing data for *O. oceanicus*, *O. gracilis*, *F. tropica*, *F. grallaria*, *N. fuliginosa*, *G. nereis*, and *Pelagodroma marina*. This produced a measure of average standardised morphometric distance within each species. All statistical analyses were conducted using SAS. Unless otherwise stated, means are reported ± 1 SD.

Capture, handling, and banding of these birds was conducted under permit from the New Zealand Department of Conservation and Animal Ethics Committee Approval.

RESULTS

Comparison of captured birds with NZSP museum specimens and other extant storm petrels

A comparison of the morphological characters of the 4 captured birds with data from the NZSP museum specimens and another 17 Southern Hemisphere storm petrel taxa is presented in Table 1. This information shows close agreement between the measurements from the captured birds with those taken from the 3 NZSP museum specimens. It also indicates that most of the taxa with which comparisons were made show little similarity to either the captured birds or the NZSP museum specimens.

Multivariate distance analysis correspondingly shows that all the NZSP museum specimens have average distances (units of standard deviation) <1 from the captured birds (NZSP museum specimens ranked 1, 4, and 9 out of 51). However, the analysis also found that *F. g. segethi* and both *O. o. oceanicus*, and *O. o. exasperatus* have average distances <1 from the captured birds (*F. g. segethi*

Table 1. Morphometrics and mass (± SD) of the 4 captured storm petrels compared with the 3 NZSP museum specimens and 17 other extant storm petrel taxa (subfamily Oceanitinae). For studies where standard deviation is not given, range is presented. Where sample size varied between measures, the range of sample size is given.

Data set	Taxa	n	Sex	wing (mm)	tail (mm)	bill length (mm)	tarsus (mm)	mid-toe + claw (mm)	mid-toe + claw/tarsus	mass (gm)
1-4	Captured birds	4	Unk	148.7 ± 3.7	66.0 ± 1.5	13.4 ± 0.3	35.9 ± 0.9	29.5 ± 1.2	0.82 ± 0.1	33.2 ± 2.5
5-7	NZSP museum specimens [1]	3	Unk	148.8 ± 2.4	59.6 ± 4.0	12.6 ± 0.1	35.1 ± 0.2	27.3 ± 0.2	0.78 ± 0.004	-
	NZSP museum specimens [2]	3	Unk	148.0 ± 0.0	64.7 ± 3.2	12.2 ± 0.3	36.0 ± 1.0	27.2 ± 0.3	0.75 ± 0.01	-
45	*O. oceanicus oceanicus* Sth Georgia, live birds [1]	12	Unk	143.3 (140.0-148.0)	62.5 (59.6-68.0)	12.5 (11.8-13.0)	34.7 (33.1-36.0)	27.5 (26.0-28.7)	0.79	-
8	*O. oceanicus oceanicus* Sth Georgia, live breeders [3]	14-22	♀	155.0 ± 3.2	-	12.6 ± 0.3	35.4 ± 1.1	-	-	36.2 ± 2.7
9		14-18	♂	150.8 ± 3.0	-	12.3 ± 0.3	34.2 ± 0.9	-	-	33.6 ± 1.9
10	*O. oceanicus oceanicus* Iles Kerguelen, live birds [4]	14	Unk	142.7 ± 5.2	-	12.4 ± 1.1	35.4 ± 1.5	-	-	34.2 ± 7.0
11	*O. oceanicus oceanicus* Iles Crozet, live birds [5]	29-31	Unk	143.0 ± 4.0	-	12.1 ± 0.4	34.8 ± 1.1	-	-	32.0 ± 3.0
12	*O. oceanicus* Atlantic skins, including juveniles [6]	97	Unk	144.9 (136.0-155.5)	63.7 (56.5-73.0)	12.6 (11.1-13.2)	34.6 (31.3-36.8)	27.5 (25.3-30.0)	0.79	-
13	*O. oceanicus exasperatus* Antarctic continent skins [7]	13-14	♀	154.6 ± 3	70.9 ± 2.8	12.2 ± 0.5	34.4 ± 0.7	29.4 ± 1.0	0.85	-
14		21	♂	151.8 ± 4.8	69.0 ± 3.4	12.2 ± 0.5	33.6 ± 1.2	28.0 ± 1.1	0.83	-
15	*O. oceanicus exasperatus* Signy I, South Orkney Is, live birds [8]	69-644	Unk	151.4 ± 3.9	69.6 ± 2.3	12.6 ± 0.7	34.2 ± 1.1	29.6 ± 1.0	0.87	37.55 ± 0.3 -46.39 ± 0.6
16	*O. gracilis gracilis* [9]	23	♀	128.2	56.3	11.1	29.5	-	-	-
17		23	♂	123.8	55.4	11.1	30.2	-	-	-
18	*O. gracilis galapagoensis* [9]	14	Unk	135.3	57.0	11.2	30.7	-	-	-
-	*O. g. galapagoensis* (single live female) [10]		-	-	-	-	-	-	-	17.0
19	*F. tropica* Antipodes and Bounty Is, skins [1]	6	♀	163.3 (158.5-167.0)	74.0 (72.0-76.0)	15.1 (14.5-15.7)	42.8 (42.0-43.5)	28.8 (27.5-29.6)	0.67	-
20		20	♂	160.0 (154.0-167.0)	73.9 (72.0-77.0)	15.1 (14.0-15.8)	41.1 (40.0-41.8)	28.2 (27.5-29.0)	0.69	-
21	*F. tropica* Signy I, South Orkney Is, live birds [11]	15-16	♀	170.8 ± 5.5	79.4 ± 3.5	15.1 ± 0.7	40.8 ± 1.2	29.3 ± 1.4	0.72	56.5 ± 3.6
22		10	♂	162.3 ± 5.0	77.6 ± 4.0	15.3 ± 0.5	39.6 ± 0.8	29.2 ± 0.1	0.74	56.0 ± 5.4
23	*F. tropica* South Shetland Is, skins [11]	6	♀	167.5 ± 3.0	77.0 ± 3.1	15.1 ± 0.6	39.3 ± 0.7	29.1 ± 0.8	0.74	-
24		9	♂	166.4 ± 4.4	74.4 ± 1.9	15.3 ± 0.6	39.6 ± 0.7	29.5 ± 1.0	0.75	-

Table 1. Continued.

25	*F. tropica* Antipodes, live birds [12]	10	Unk.	164.3 ± 12.0	75.3 ± 8.5	15.2 ± 0.9	41.3 ± 5.4	30.2 ± 3.2	0.73	53.9 ± 12.0
26	*F. tropica* Iles Crozet, live birds [5]	38-54	Unk.	163.0 ± 5.0	-	15.4 ± 0.6	40.9 ± 1.4	-	-	52.0 ± 3.0
27	*F. tropica* Iles Kerguelen, live birds [4]	13	Unk.	171.4 ± 6.9	-	15.8 ± 1.2	42.5 ± 1.8	-	-	54.4 ± 6.1
28	*F. g. grallaria* Lord Howe I, live birds, wing not straightened [13]	35-37	Unk.	168.0 ± 3.8	75.6 ± 3.3	14.1 ± 0.4	37.1 ± 1.0	-	-	52.0 ± 4.7
29	*F. g. grallaria* Lord Howe I, skins [14]	8	Unk.	165.0 ± 3.0	75.0 ± 2.5	14.0 ± 0.5	37.6 ± 1.3	21.6 ± 1.1	0.57	-
30	*F. g. titan* Rapa I, skins, range for male and female [15]	10	♀	184.1	83.8	15.5	41.6	25.8	0.62	-
31		17	♂	181.0 (177-188)	82.4 (78.0-89.0)	15.4 (15.0-16.3)	40.6 (39.0-43.0)	25.1 (23.6-27.0)	0.62	-
32	*F. g. segethi* Mas Atierra, Juan Fernandez Is, range for both male and female [1]	12	♀	156.4	73.5	13.4	35.6	21.5	0.60	-
33		51	♂	155.4 (146.0-163.0)	73.3 (71.0-77.0)	13.1 (12.6-14.0)	35.0 (33.0-37.0)	21.6 (20.0-22.6)	0.62	-
34	*F. g. leucogaster* Tristan da Cunha, live birds [16]	24-30	Unk.	168.0 ± 3.8	78.3 ± 3.8	15.8 ± 0.6	40.7 ± 2.7	26.1 ± 2.7	0.64	52.6 ± 4.7
35	*Nesofregetta fuliginosa* Line Group and Marquesas Is, skins [17]	5	♀	183.2	95.1	16.2	42.0	30.6	0.73	-
36		8	♂	186.0 (179.0-194.0)	96.0 (94.0-100.0)	17.3 (16.6-18.0)	41.6 (40.0-44.0)	30.6 (29.0-34.0)	0.74	-
37	*G. nereis* Iles Kerguelen, live birds [4]	38-41	Unk.	126.8 ± 3.8	-	13.1 ± 0.9	31.9 ± 1.3	-	-	38.2 ± 3.5
38	*G. nereis* Iles Crozet, live birds [5]	16-18	Unk.	127.0 ± 6.0	-	13.6 ± 0.7	32.6 ± 1.4	-	-	32.0 ± 5.0
39	*G. nereis* Chatham I, live birds [18]	11-16	♀	134.9 ± 3.1	66.0 ± 2.4	13.0 ± 0.3	32.3 ± 0.9	-	-	34.0 ± 2.9
40		13-19	♂	129.5 ± 2.5	63.4 ± 1.9	12.7 ± 0.4	31.8 ± 1.1	-	-	34.0 ± 2.9
41	*G. nereis* New Zealand sub-Antarctic Is, skins [14]	24-27	♀	133.2 ± 3.7	67.0 ± 3.0	12.9 ± 0.4	33.4 ± 1.4	-	-	-
42		16-17	♂	127.4 ± 3.6	62.9 ± 2.1	13.0 ± 0.5	31.7 ± 1.5	-	-	-
47	*Pelagodroma marina marina* Tristan da Cunha, skins [19]	1	♀	166	80.5	16.7	41.1	35.8	0.87	-
48		1 ?	♂	159	80.2	15.0	42.1	33.1	0.79	-
43	*Pelagodroma marina maoriana* New Zealand region, skins [19]	21	♀	158.0 (149.0-169.0)	76.7 (67.0-83.7)	15.7 (14.6-16.7)	40.8 (37.8-43.0)	35.1 (32.0-37.5)	0.86	-
44		15	♂	157.3 (150.0-164.0)	74.8 (68.9-85.7)	15.8 (14.9-16.5)	40.8 (38.5-42.4)	35.0 (32.6-40.9)	0.86	-
46	*Pelagodroma marina maoriana* Mokohinau Is, New Zealand, live birds [20]	9	Unk.	158.3 ± 4.1	-	16.7 ± 0.7	-	-	-	46.9 ± 4.1

Table 1. Continued.

49	*Pelagodroma marina dulciae* Australia, skins[19]	13	♀	157.5 (151.0-167.0)	74.0 (70.5-77.6)	16.8 (15.2-17.6)	42.2 (40.8-44.0)	36.0 (34.0-37.6)	0.85	-
50		19	♂	159.2 (152.0-168.0)	73.8 (69.0-82.8)	16.8 (16.0-18.0)	42.0 (40.0-43.9)	36.5 (34.9-38.2)	0.87	-
51	*Pelagodroma marina albiclunis* Kermadec Is, skins[19]	1-4	♀	160.3 (155.0-166.0)	73.8 (72.6-76.3)	16.7	41.7 (41.0-42.3)	37.0 (35.2-38.0)	0.89	-
52		11	♂	155.0 (144.0-163.0)	70.1 (66.3-73.5)	16.6 (15.3-17.7)	40.8 (37.5-43.1)	37.0 (35.9-39.3)	0.91	-
53	*Pelagodroma marina hypoleuca* Canary Is and Madeira, skins[19]	3	♀	161.0 (156.0-170.0)	76.0 (72.7-79.0)	16.7 (16.2-17.7)	43.9 (42.6-44.8)	35.8 (35.2-36.7)	0.82	-
54		3	♂	156.3 (151.0-160.0)	70.1 (66.0-73.7)	17.0 (16.6-17.7)	43.2 (42.6-43.5)	35.7 (34.9-37.2)	0.83	-
55	*Pelagodroma marina eadesi* Cape Verde Is, skins[19]	20	♀	161.1 (151.0-170.0)	73.7 (68.0-79.5)	18.1 (17.4-19.5)	45.0 (43.0-47.5)	36.3 (34.3-38.4)	0.81	-
56		20	♂	157.8 (151.0-166.0)	71.4 (68.3-77.5)	18.0 (17.0-18.9)	44.4 (41.7-48.9)	36.0 (33.4-37.9)	0.81	-

Table 1. Continued. [1] Murphy & Snyder 1952, [2] Bourne & Jouanin 2004, [3] Copestake & Croxall 1985, [4] Weimerskirch *et al*. 1989, [5] Jouventin *et al*. 1985, [6] Murphy 1918, [7] Roberts 1940 (corrected by Beck & Brown 1972), [8] Beck & Brown 1972, [9] Murphy 1936 (taken from Brooke 2004), [10] Harris 1969, [11] Beck & Brown 1971, [12] Warham & Bell 1979, [13] ABBBS, reported in Marchant & Higgins 1990, [14] Marchant & Higgins 1990, [15] Murphy 1928, [16] Fraser *et al*. 1988, [17] Murphy 1924, [18] Imber reported in Marchant & Higgins 1990, [19] Murphy & Irving 1951, [20] B. Stephenson, *unpubl*.

ranked 2 and 3 (Table 1, data set 32 and 33, respectively); *O. oceanicus* ranked 5, 6, 7, 8, 10, 11, 12, and 13 out of 51 (Table 1, data set 12, 45, 15, 8, 10, 9, 11, and 13, respectively)). Therefore, these taxa are indistinguishable from the captured birds based on the measurements analysed (wing, bill, and tarsus lengths). However, all other taxa within *F. tropica*, *F. grallaria*, *N. fuliginosa*, *G. nereis*, and *Pelagodroma marina* were significantly different to both the captured birds and the NZSP museum specimens, falling outside of this grouping (having average distances >1). Additionally, *Pelagodroma marina*, *G. nereis*, and *O. gracilis* all fall out as distinct groups, not forming an overlap with any other taxa.

Unfortunately, the data is limited for several of the *O. o. oceanicus* studies, with no measurements for tail length, mid-toe + claw (therefore leaving mid-toe + claw/tarsus ratio undeterminable) (see Table 1). This led to a lack of resolution between the captured birds, the NZSP museum specimens, and taxa from *O. oceanicus*, and *F. grallaria*. To resolve this grouping we examined mean mid-toe + claw/tarsus ratio (from those taxa for which this could be determined) and 6 other plumage and structural characters (Table 2) (see Appendix 1). The comparison in Table 2 clearly resolves the lack of resolution suggested by Table 1, with the captured birds and the NZSP museum specimens sharing all 6 plumage and structural characters examined, but *O. oceanicus*, *F. tropica*, and *F. grallaria* differing in 3, 2, and 5 characters, respectively. Furthermore, the mean mid-toe + claw/tarsus ratio of the captured birds differed significantly to *F. tropica* and *F. grallaria*, and although still significantly different to that of *O. oceanicus*, this difference was less. The captured birds also differed significantly from the NZSP museum specimens, with the former being slight larger, and this will be discussed later.

Appendix 1 contains a complete description of the plumage and structural characters of the captured birds, NZSP museum specimens, *O. oceanicus*, *F. tropica*, and *F. grallaria*. This comparison shows that in a number of other subtle ways, the captured birds and NZSP specimens are clearly different to the other taxa examined. The long narrow toes of NZSP agree more closely with *O. oceanicus*, as noted by Mathews (1932; 1933). There seems to be a gradation in the toes/claws of these taxa, from the flattened and short toes, with relatively blunt, flattened, and almost round claws of *F. grallaria*; to rather less flattened and relatively

Table 2. Plumage and structural character descriptions of the captured birds, the NZSP museum specimens, *O. oceanicus*, *F. tropica* and *F. grallaria*.

Character	Captured birds	NZSP museum specimens	*O. oceanicus*	*F. tropica*	*F. grallaria*
Webs of feet black	Y	Y	N	Y	Y
Toes narrow and claws unflattened	Y	Y	Y	Y	N
Relative toe length (longest to shortest = middle, outer, inner)	Y	Y	Y	N	N
Basal colour of chin and throat feathers pale	Y	Y	N	Y	N *
Pale bases to primary feathers	Y	Y	Y	N	N
Concealed white base to both inner and outer web of outer rectrices	Y	Y	N	Y	N
Number of character differences from captured birds	-	None	Three	Two	Five
Mean mid-toe + claw/tarsus ratio for the species	0.82 ± 0.05	0.77 ± 0.02	0.83 ± 0.04	0.72 ± 0.03	0.61 ± 0.02

* based on *F. g. grallaria*, but note differences with *F. g. titan*

longer toes of *F. tropica*; to the long narrow toes of NZSP (Fig. 1); to the long slender toes of *O. oceanicus*. However, toe shape should be used cautiously as a distinguishing characteristic, as the differences seen within *Fregetta* are substantial compared to those between NZSP and *F. tropica*. The webs of the feet in both *O. oceanicus* and *O. gracilis* are coloured (Zink & Eldridge 1980), whilst those of both *Fregetta* spp. and NZSP are black.

The bill shape of NZSP (Fig. 2) is distinctly more like that of *Fregetta*, being slightly down-curved with a bulbous but sharply hooked tip, quite unlike the fine, straight bill of *Oceanites* and *Garrodia*. While these features are not as extreme in NZSP as in *F. grallaria*, they certainly share some similarities. It would be useful to have more material (photos, drawings, descriptions) from live birds of both *Fregetta* and *Oceanites*, as comparisons with museum specimens are limited. Comparison of the nostrils of the captured birds with those of the other taxa again suggest that they are structurally more like *Fregetta* than *Oceanites*, having the distal end raised more prominently from the culminicorn, with the opening directed upwards at a greater angle.

The streaked underparts of NZSP also represent a feature found consistently in this species (Fig. 3), but not in any of the other taxa examined. This streaking appears to vary from bird to bird and may allow individual recognition from examination of photographs of wild birds.

As might be expected from differences in the morphological structure of this species, the flight progression of NZSP is distinctive, being generally close to the sea surface, with a rapid, erratic, and swiftlet-like character. Whilst similar to *O. oceanicus*, they generally appear to sweep across the surface more and are less buoyant. Their flight behaviour therefore often renders them inconspicuous. The combination of these features sets them apart from all storm petrel taxa whose range they share (Fig. 4).

Of particular importance in distinguishing between *F. tropica* and *F. g. grallaria* is the colour of the base of the feathers on the throat (Marchant & Higgins 1990; pers. obs.). *F. g. grallaria* has feathers which are completely dark, as does *O. oceanicus*. Contrastingly, however, examination of *F. g. titan* shows that this taxon has pale windows to the dark feathering of the throat. Both *F. tropica* and NZSP also have dark feathers with pale central windows on either side of the rachis. Although the throat feathers of *F. tropica* and NZSP show a similar

Fig. 1. Long narrow toes and unflattened claws typical of NZSP. Photo of B-94503, captured 5 Jan 2006. Photo by Rohan Clarke.

Table 3. Range of morphological variation found within recognised storm petrel taxa from the Southern Hemisphere (subfamily Oceanitinae). Data derived from studies shown in Table 1.

Storm petrel species	Number of recognised subspecies/number included in the analysis	Number of studies sampled in the analysis	Average standardised morphometric distance
Captured birds and NZSP museum specimens combined	-	-	0.554 ± 0.254
O. oceanicus	2 / 2	7	0.528 ± 0.254
O. gracilis	2 / 2	3	0.588 ± 0.226
F. tropica	2* / 1	6	0.586 ± 0.224
F. grallaria	4 / 4	5	1.468 ± 0.789
N. fuliginosa	0 / 1	1	0.640
G. nereis	0 / 1	4	0.472 ± 0.166
Pelagodroma marina	6 / 6	7	0.820 ± 0.403

* Debate continues over the existence of *F. tropica melanoleuca* and its placement within *F. tropica*.

(but not identical) pattern, in both species they are distinctively different to *O. oceanicus*.

Another character separating NZSP and *F. g. grallaria* is the concealed white bases to the outer rectrices. Both *F. tropica* and NZSP share similarly patterned white inner and outer webs at the bases of these feathers, whilst *F. g. grallaria* and *O. oceanicus* have a slightly differently shaped white pattern only on the inner web, the outer web being dark.

Lastly, the overall plumage colouration should be highlighted with reference to *O. oceanicus* and the 2 *Fregetta* spp. The underwing pattern shown in the drawing of the NZSP type in Mathews (1933) shows the outer webs of the median under primary coverts as dark, with white inner webs, and this feature was seen in the captured birds, and was clearly visible in photographs of birds in the field (Flood 2003; Gaskin & Baird 2005). It appears to be diagnostic of the species. Moreover, the patterning of pale and dark feathers in the undertail coverts points to a species different from the other black-and-white storm petrels.

Fig. 2. Closeup of the head and bill of B-94504, captured 6 Jan 2006. This photo shows the typical sloping forehead of NZSP, as well as the bill and nostril structure. Photo by Rohan Clarke.

To examine our assertion that the captured birds and NZSP museum specimens represent a distinct species, separable from other storm petrel taxa, we conducted a further analysis to determine the level of variability within the morphological characters of other recognised storm petrel species (Table 3). This analysis investigated the average standardised morphometric distance for the 7 species shown in Table 3, and found considerable morphological variation within these currently recognised species of storm petrel. The level of variation discovered varied from 1.468 ± 0.789 in *F. grallaria*, to 0.472 ± 0.166 in *G. nereis*. The combined value for the captured birds and NZSP museum specimens showed a relatively low variation of 0.554 ± 0.254, less than all other taxa except for *O. oceanicus* and *G. nereis*. Of note is the amount of variation within *F. grallaria*, which is considered a single species containing 4 sub-species. It appears that each of these taxa falls along a size gradient, suggesting individually identifiable populations based on morphology alone exist.

Overall, the characters examined show that the captured birds and the NZSP museum specimens are the same species, which is distinct from all other taxa examined.

Feather Lice (Insecta: Phthiraptera)

One feather louse was collected from the back of B-97715, and 1 from the underside of each wing at the base of the primaries of B-94503. All 3 lice (1

Fig. 3. Two photos showing the streaked underparts of NZSP. Left is B-94503 and right is B-94505. These birds are considered moderately streaked individuals, with B-94503 having slightly heavier streaking. Photos by Rohan Clarke and Halema Jamieson, respectively.

male and 2 female) were identified as *Philoceanus fasciatus* (Carriker, 1958)(Fig. 5).

Age and breeding status of captured birds
All 4 birds had downy brood patches and were scored as 0. B-94504 had several body feathers adjacent to the brood patch just erupting from pin, but this may have simply been due to the body moult it was undergoing.

DISCUSSION

As the analysis above has shown that the captured birds and the NZSP museum specimens represent the same species, we now refer to them both as the New Zealand storm-petrel (NZSP).

Morphological analysis and comparison of NZSP with other extant storm petrels
The multivariate analysis shows that the 4 captured birds are most similar to the 3 NZSP museum specimens, *O. oceanicus*, and *F. g. segethi*. A lack of additional morphological data for many taxa meant that this grouping could not be further resolved using statistical analysis. It is not surprising that this grouping included *O. oceanicus*, with which NZSP has often been considered to have a close taxonomic relationship based on morphology (Murphy & Snyder 1952), being variously considered as a genetically-based plumage variant of *O. oceanicus* (Murphy & Snyder 1952) or as a separate species *O. maorianus* (Oliver 1955). However, the inclusion of *F. g. segethi* was more of a surprise, clearly due to the similarity in the measures examined (wing, bill, and tarsus length). That 2 genera were shown to be morphologically indistinguishable from NZSP in the statistical analysis shows how similar these storm petrel species are with respect to morphology. However, it does not take into account the additional differences in the plumage and structure examined in Table 2.

All other taxa examined in the analysis were significantly different with respect to morphology. This confirms that the NZSP is distinct from these other taxa, and it should be noted, from all other *F. grallaria* subspecies (*F. g. grallaria, F. g. titan, and F. g. leucogaster*). Clearly there are other differences between NZSP and *Pelagodroma marina*, but this taxon was included for completeness, and due to size comparisons made with the suspected NZSP during early field observations. Moreover, these results in general also support assertions that birds observed in the field were smaller than both *Fregetta* species (Saville et al. 2003; Gaskin & Baird 2005). Interestingly, according to the analysis, *Pelagodroma marina, G. nereis*, and *O. gracilis* all fell out as distinct groups in the morphological analysis, not overlapping with any other taxa, giving strong support for their distinctiveness.

Structural and plumage comparison of NZSP with other extant storm petrels
Comparison of additional plumage and structural characters (Table 2) enabled us to demonstrate the similarity between the captured birds and the NZSP museum specimens, whilst differentiating them from all taxa of *O. oceanicus, F. tropica* and

Fig. 4. Two different NZSPs in flight, showing the underparts (taken 5 Jan 2006) and upperparts (taken 6 Jan 2006). Photos by Brent Stephenson.

F. grallaria. Even *O. oceanicus* and *F. grallaria*, of which some taxa examined were indistinguishable based on the multivariate analysis (see above), were separated by at least half of the 6 characters examined. It is our opinion that had a complete dataset been available for the multivariate analysis, this would probably have eliminated any *Fregetta* taxa from the grouping. However, the mean mid-toe + claw/tarsus ratio for *O. oceanicus* fell very close to that of the captured NZSP. Furthermore, the significant difference between the captured birds and the NZSP museum specimens is perhaps as a result of shrinkage (Bretagnolle *et al.* 1991), or the difficulty in accurately measuring the toe + claw length once specimens have hardened.

The further comparison of the characters examined in Appendix 1 showed additional differences between the NZSP and the other taxa examined. The long narrow toes, shape and structure of the bill and nostrils, streaked underparts, and flight progression, were particularly important in this analysis.

The examination of storm petrel specimens at the Museum of New Zealand Te Papa Tongarewa, Auckland Institute and Museum, and the British Natural History Museum shows a great deal of variability exists in the patterning of the breast and belly of *F. tropica*, but no bird showed patterning

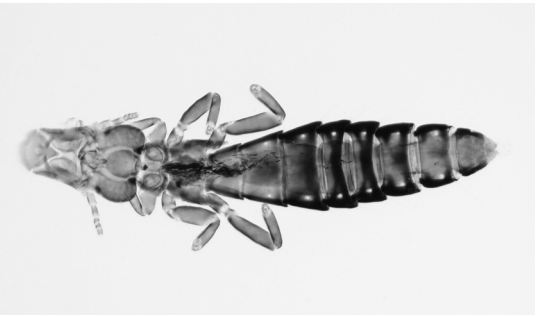

Fig. 5. Male *Philoceanus fasciatus* (Carriker, 1958) collected from B-97715 at Waimaomao Bay, Little Barrier Is, 4 Nov 2005 by Richard Griffiths. Photo by Jean-Claude Stahl.

remotely similar to the streaking seen in NZSP. The only truly streaked *F. tropica* collected to date is the Samoan specimen of *Thalissidroma lineata* (Peale 1848; Murphy & Snyder 1952). Similarly, there are almost no records of *F. grallaria* showing similar streaked underparts, except for the Marquesan specimen (Murphy 1924; Murphy & Snyder 1952). Even intermediate or dark morph individuals evident in some populations of *F. g. grallaria* (Lord Howe and Kermadec Islands) are not streaked but show gradual darkening of the plumage in the axillaries and flanks, with the belly remaining pale in all but the darkest individuals (Marchant & Higgins 1990; *pers. obs.*). Occasional aberrantly plumaged *O. oceanicus* have been recorded (Murphy 1918; Murphy & Snyder 1952; Oliver 1955; Trimble 1968; Bourne 1987; Curtis 1988). However, these have not shown streaking on the lower-breast and belly. To date, there has been no record of any population of storm petrel that shows similar prominent streaking to that found in the NZSP.

Morphological variation currently accepted within other storm petrel species

The statistical analysis of morphological variation within accepted storm petrel species showed that variation found within the NZSP (including captured birds and museum specimens) to be less than that found within both species of *Fregetta*, *N. fuliginosa*, *O. gracilis*, and *Pelagodroma marina*. Only *O. oceanicus* and *G. nereis* showed less variation. Clearly the variation found within and between the captured birds and the NZSP museum specimens is within the limits of currently accepted storm petrel species, and in many cases much less.

It is interesting that we found a relatively low amount of variation in *O. oceanicus*, as it is generally considered that this species has 2 distinct sub-species, but our results suggest that this may be clinal and related to latitude, rather than to actual separable sub-specific differences (see Brooke 2004). *G. nereis* is generally considered to be monotypic,

and our analysis supports this, with this species having the lowest amount of morphological variation. Furthermore, the relatively high variation found within *F. grallaria* would suggest this species needs urgent review. Our data would suggest that the variation found within this species is much higher than that found within any other storm petrel species examined, and may indicate that some taxa within this species warrant full species status. The plumage variation in *F. g. titan*, mentioned above, suggests that further plumage variation may exist within the *F. grallaria* complex.

Feather Lice (Insecta: Phthiraptera)

Evidence for a taxonomic link between NZSP and *Fregetta* is provided by the *Philoceanus fasciatus* collected from 2 of the captured NZSP. The louse genus *Philoceanus* Kellogg, 1903 presently contains 6 valid species, all parasitic on storm petrels (Price *et al*. 2003). *Philoceanus fasciatus* has been previously recorded from both *F. tropica* and *F. grallaria* and is morphologically very different from both *Philoceanus robertsi* (parasitic on *O. oceanicus*) and *Philoceanus garrodiae* (on *G. nereis*) (Clay 1940; Timmermann 1961; Clay & Moreby 1967).

Co-speciation of hosts and their lice has been found to be relatively common among petrels and albatrosses (Paterson *et al*. 2000; Page *et al*. 2004). If the host-parasite association between the NZSP and the louse *Philoceanus fasciatus* was regarded as an indication of phylogenetic relationship, it would again indicate that the NZSP is more closely related to *Fregetta* than to either *Oceanites* or *Garrodia*.

Age and breeding status of the captured birds

The downy brood patches of all 4 birds indicated that they were not breeding when caught. Non- or pre-breeding storm petrels captured near breeding colonies may exhibit bare brood patches (Allan 1962; Beck & Brown 1972; McFarlane Tranquilla *et al*. 2003), whilst brood patches of breeding storm petrels begin denuding about a month before egg-laying (*O. castro* 20-40+ days: Allan 1962; European storm-petrel *Hydrobates pelagicus* < 30 days: Lockley 1983; *F. tropica* ~30 days: Beck & Brown 1971; *O. oceanicus* 30-50 days: Beck & Brown 1972). Regrowth of the down differs between species with respect to hatching date (*O. castro* within a few weeks: Allan 1962; *O. oceanicus* 55 + days: Beck & Brown 1972). First year *H. pelagicus* rarely visit breeding colonies, and only at 2 years old are they often recaptured at colonies (Okill & Bolton 2005; see Cramp 1998 for other species). Given that the 3 birds captured in Jan did not show any sign of brood patch denudation, when they should have if visiting a breeding colony, it is likely that these birds were immature and of pre-colony-visiting age. Based on arrival and departure dates of these birds in the Hauraki Gulf, we suggest birds should be incubating eggs during Dec and Jan.

An unravelling taxonomy

Through the comparison of morphometric data and plumage characteristics presented here, it is evident that the recently captured storm petrels and the NZSP museum specimens are the same species. Furthermore, the NZSP is distinct from all other storm petrel taxa examined in this study, including *O. oceanicus*, which implies that Murphy & Snyder (1952) were incorrect in their assessment of the 3 specimens as being a "*Pealea*" phase of *O. oceanicus*. Molecular work to investigate the relationships between these *Fregetta* spp. and links to *Pealeornis* is warranted.

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Appendix 1. Comparison of plumage characteristics and structure of the 4 captured storm petrels with the 3 NZSP museum specimens and other similar extant black-and-white storm petrel species (NB. comparison is made only with *F. g. grallaria* as differences between this and other sub-species of *F. grallaria* have been recognised, but are not well documented). Fig. 1-4 are provided for reference.

	Captured birds	NZSP	*O. oceanicus*	*F. tropica*	*F. g. grallaria*
Toe lengths (long - short)	Middle, outer, inner	Middle, outer, inner	Middle, outer, inner	Outer, middle, inner	Outer, inner, middle
Bare parts					
Bill	Black; latericorn broadest near base of bill, narrowing gradually towards tip, tomia has slight 's' curve; lower edge of ramicorn tends to curve downwards, giving bill drooping decurved appearance, area of least depth distinct being just forward of where nostril joins culminicorn, increasing into slightly bulbous maxillary and mandibular unguis, but with sharply hooked tip	Black; latericorn broadest near base of bill, narrowing gradually towards tip, tomia has slight 's' curve; lower edge of ramicorn tends to curve downwards, giving bill drooping decurved appearance, area of least depth distinct being just forward of where nostril joins culminicorn, increasing into slightly bulbous maxillary and mandibular unguis, but with sharply hooked tip; shrinkage means mandibular unguis not as pronounced as in live birds	Black; latericorn broadest forward of base of bill being slightly oval in shape, but narrowing gradually towards tip, tomia is therefore curved; lower edge of ramicorn fairly straight giving uniform depth along length of bill, with no distinct narrowing, mandibular unguis unpronounced, sharply hooked tip	Black; latericorn wide at bill base tapering sharply towards tip, tomia has pronounced 's' curve; lower edge of ramicorn tends to curve downwards, area of least depth distinct being just forward of where nostril joins culminicorn, increasing into slightly bulbous maxillary and mandibular unguis, but with sharply hooked tip	Black; latericorn wide at bill base and almost triangular in shape, tapering towards bill tip, tomia has pronounced 's' curve; lower edge of ramicorn straight until forward of nostril, then mandibular unguis bulbous and curves downwards, giving bill slightly drooping decurved appearance, but sharply hooked tip; area of least depth distinct, being below where nostril joins culminicorn
Nostril	Black; nostril approximately 40% of bill length, opening points forwards and upwards (c.35° from line of bill) and is slightly lifted from culminicorn, septum does not reach opening, soft to touch	Black; shrinkage leaves comparison with captured birds difficult; shrinkage of nostril more pronounced than in other extant *Oceanites* and *Fregetta*	Black; nostril approximately 40% of bill length, opening points forwards and upwards (c.30 ° from line of bill) and is slightly lifted from culminicorn, septum does not reach opening [3]	Black; nostril approximately 50% of bill length [3], opening points forwards and upwards (c.40° from line of bill) and is prominently lifted from culminicorn, septum unknown	Black; nostril approximately 50% of bill length, opening points forwards and upwards (c.30° from line of bill) and is lifted from culminicorn, septum does not reach opening [3]
Tarsi	Black; booted tarsi	Black; booted tarsi	Black; booted tarsi	Black; booted tarsi	Black; scutellated tarsi
Feet/webs	Black feet; black webs, visibly dark in field	Black feet; black webs, some suggestion the feet and webs of the Paris specimens were painted black [1]	Black feet; webs have yellow-orange pale patches; visible in the field and in specimens	Black feet; black webs	Black feet; black webs
Toes/claws	Narrow toes; claws slightly flattened, broadest point closer to base than tip, 1.5 times as long as wide; sharp tip, no sign of wear (in pre-breeders)	Narrow toes; claws slightly flattened, broadest point closer to base than tip, 1.5 times as long as wide	Narrow toes; claws flattened, broadest point closer to tip than base[3], 2 times as long as wide	Narrow toes; claws flattened and spade-shaped, less than 1.5 times longer than wide when unworn, becoming more oval when worn	Flattened wide toes; claws flat and wedge-shaped, slightly longer than wide when unworn, almost round when worn [3]
Plumage					
Head	Black/blackish-brown, two with small pale loral patch (B-97715 and B-94503) and one with single white feather on nape (B-94505)	Black/blackish-brown	Black/blackish-brown, juveniles often show white loral patch [2]	Black/blackish-brown	Black/blackish-brown
Throat	Feathers predominantly white at base, with black/blackish-brown tips giving dark throated appearance unless feathers parted or worn	Feathers predominantly white with black/blackish brown tips; Tring specimen has a mottled, pale throated appearance due to wear, not as apparent in the Paris specimens	Feathers completely dark, predominantly blackish brown with dark grey bases	Feathers dark brown at base and tip, with a white central window on each side of the feather, with dark usually extending between the base and tip along the rachis	Feathers completely dark, predominantly black/blackish brown with brownish grey bases; *F. g. titan* has white central windows, similar to *F. tropica*

Appendix 1. Continued.

Upperwing	Generally black/blackish brown, with remiges darker than coverts; secondaries when new appear to have pale fringes (B-97715), the median and greater coverts appeared paler as a result of wear on B-97715 and B-94503, but in birds observed at sea these feathers have pale fringes (possibly when fresh) which also make this area show as a pale carpal bar	Black/blackish brown, remiges darker than coverts, but unable to open wing to examine fully	Remiges black-brown, contrasting with paler greyish or greyish brown greater coverts forming a usually pronounced carpal bar across innerwing [3]	Mainly black-brown, outer secondaries tipped white, all coverts dark brown, with greater coverts narrowly fringed white, median coverts less so, marginal coverts narrow dark-brown fringes; when worn white fringes lost and greater and median coverts dark brown; upperwing patterning forms inconspicuous grey-brown bar from carpal to base of wing at rear [3]	Blackish with narrow white fringes to median coverts and greater coverts, latter paler greyish brown appearing as pale wingbar on innerwing becoming paler with wear; pale fringes reduce with wear; blackish remiges and forewing; upperwing in fresh plumage has frosted appearance from pale fringes to coverts [3]
Underwing	Remiges dark grey-brown, greater under primary coverts dark grey with broad pale fringes, innermost feathers paler grey, median under primary coverts have distinct blackish brown outer webs and white inner webs (seen as dark projections into white of underwing in photos of birds in flight); marginal and lesser coverts blackish brown, contrasting with white median and greater underwing coverts; axillaries mostly white or pale grey, feathering towards leading edge of armpit blackish brown	Difficult to ascertain from closed wing, "underwing coverts brownish black, axillaries white; quills below ashy grey" [4], however, the drawing of the type in Mathews (1933) shows several of the diagnostic features apparent in the captured birds – dark outer webs to the median under primary coverts, pale grey greater under primary coverts with broad pale edges	Blackish brown throughout, although many show pronounced pale flash on inner underwing coverts [3]	Remiges dark grey-brown, greater under primary coverts dark grey with broad white fringes, median under primary coverts have dark and white outer and inner webs to base of feathers (similar to captured birds), respectively, but white tips and lesser under primary coverts blackish brown; marginal underwing coverts dark brown, and lesser, median and axillaries white [3]	Remiges and outer four greater under primary coverts dark grey with pale fringes, secondaries very narrow white fringes; outer median under primary and lesser under primary coverts black-brown on outer web and white on inner (similar to captured birds) with white tips; lesser underwing coverts black-brown; remaining median and greater underwing coverts white [3], thus forming white triangular patch in underwing
Base of primaries	Concealed white bases to otherwise dark feathers (as above)	Concealed white bases to otherwise dark feathers (as above)	Concealed white bases to otherwise blackish brown feathers [3], examination of museum specimens shows dark bases	Completely dark feather, no concealed pale base	Completely dark feather, no concealed pale base
Upperparts	Mantle, back, scapulars, and tertials black/blackish brown; rump predominantly blackish brown with some white and pied feathers extending onto white uppertail coverts; back feathers may have narrow whitish tips when fresh (B-97715)	Black/blackish brown above, with white rump and uppertail coverts; "a few feathers of the lower back indistinctly fringed with whitish" [4]	Entirely blackish brown, except for broad U-shaped band of white across lower rump and uppertail coverts [3]	Mantle and back dark brown, rump black-brown; when fresh feathers broadly fringed white on rump, narrowly on mantle, scapulars dark brown; uppertail coverts white [3]	Mantle and back blackish brown, when fresh all feathers have obvious white fringes lost with wear; uppertail coverts white, except in dark morph where only lateral feathers are pale [3]
Underparts	Upper-breast black/blackish brown, with white lower-breast, belly, flanks, and vent, moderately to heavily streaked blackish-brown; streaking is due to feathers with dark shafts and adjacent variable dark webs; sides of breast and belly generally more heavily streaked than central area and flanks, often forming dark thigh patches; highly variable amongst individuals; dark upper- and white lower-breast not well demarcated, with blackish-brown projecting into the white belly	Upper breast blackish brown; lower-breast and belly white and with blackish brown streaking; the two Paris specimens differ in the distribution of streaking, having less immaculate white near the midline than the Tring specimen	Mostly black-brown, except for white extending from lower rump and uppertail coverts down onto lower flanks; belly dark brown; juveniles often have white fringes to the feathers of the belly [2]	Variable; upper-breast dark-brown contrasting with white lower-breast/belly and flanks; sometimes clear demarcation, usually with dark brown line running down centre of belly, although this varies from complete solid line, to broken line, to being almost non-existent (varies between island populations)	Variable; light morph has dark-brown upper breast with sharp demarcation to white lower breast/belly; intermediate to dark morph has increasing amount of dark brown from flanks to belly, with darkest individuals having completely dark brown underparts except smudgy white centre of belly; centre of the belly never shows dark patterning like *F. tropica*

Appendix 1. Continued.

Tail	Black/blackish brown above and below; bases of all except the two central rectrices have concealed white inner and outer webs, inner being more extensive, reaching almost half the feather's length; each rectrix narrow	Black/blackish brown above and below; concealed bases of all except two central rectrices have white inner and outer webs, inner being more prominent; each rectrix narrow	Black-brown above and below; only inner webs of outer rectrices have concealed white bases extending almost half the length of the feather, outer web is dark; each rectrix narrow	Black brown above and below; inner and outer webs of outer rectrices have concealed white bases, inner more prominent extending almost half the length of the feather; each rectrix narrow	Black/blackish brown above and below; only inner webs of outer rectrices have concealed white bases, outer web is dark; each rectrix broad and paddle shaped
Undertail coverts	Predominantly black/blackish brown with white bases; in 2 birds narrow white tips to the dark lateral greater coverts; in 2 this is less obvious, possibly through wear; also seen in birds photographed at sea	Predominantly black/blackish brown, with white bases, some pale fringing	Predominantly black brown, but lateral undertail coverts white	Dark brown, lateral feathers narrowly fringed with white [3]	Dark brown, except lateral feathers which are white; intermediate and dark morphs are predominantly dark in this area [3]
Structure	Head has sloping forehead. Body appears slim, wings usually appear sharply pointed in travelling flight, becoming more rounded when feeding or manoeuvring. Tail square to slightly rounded when spread. Feet project prominently past tail in flight	Difficult to ascertain head/forehead shape. Difficult to ascertain body and wing shape from specimens. Tail square to slightly rounded when spread. Feet project prominently past tail	Bulbous forehead with rounded peak forward of eye. Body appears slim, wings usually appear sharply pointed in travelling flight, less so when feeding. Tail square or slightly forked [3] Feet project slightly past tail in flight	Bulbous forehead with rounded peak forward of eye. Body appears chubby, wings broad but slightly pointed in travelling flight, more rounded when feeding. Tail square [3] Feet project c.1 cm beyond tail in flight [3]	Bulbous forehead with rounded peak forward of eye. Similar body shape and wing profile as *F. tropica.* Tail square to slightly rounded when spread [3] Feet do not project past tail in flight [3]
Flight progression and jizz	Travelling flight strong, direct, low to water, some gliding, very similar to swiftlets; feeding flight slower, with surface dipping and glides, wings held moderately high over back in V, frequently kicking off the sea as it moves over surface; frequent abrupt changes of direction		Travelling flight strong and direct, with rapid wing-beats interspersed with short glides, similar to swiftlets; feeding flight slower, patter, walk, and jump on surface with wings held high over back in V and legs dangling or 'anchored' in surface[3]	Flight erratic and zig-zagging but broad-winged with slow wingbeats; wings appear broader when gliding; during feeding flight swing wildly over surface frequently kicking off but not often pattering on surface, wings sometimes held in only shallow dihedral [3]	Flight and feeding pattern similar to *F. tropica*;

[1] Murphy & Snyder (1952), [2] Murphy (1918), [3] Marchant & Higgins (1990), [4] Mathews (1932), but much of the material presented is also taken from examination of specimens held at the Museum of New Zealand Te Papa Tongarewa and Auckland Museum, NZ.